FIELD STUDIES OF MINERAL NUTRITION OF *LARREA TRIDENTATA*: IMPORTANCE OF N, pH, AND Fe

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ABSTRACT.— Multivariate analysis of soil and plant data from the northern Mojave Desert was used to investigate aspects of the mineral nutrition of *Larrea tridentata* (Sesse & Moc. ex DC.) Cov. *Larrea tridentata* biomass was significantly correlated with soil NO_3 and pH and leaf Fe content. Leaf cation accumulation was negatively correlated with leaf Fe concentration.

There are several hypotheses for the often strikingly discontinuous distribution of *Larrea tridentata* (Sesse & Moc ex DC.) Cov. in southwestern U.S. deserts. Beatley (1974) suggested that absence of *L. tridentata* from playas of the Nevada Test Site in the northern Mojave Desert is due to limiting cold during winter temperature inversions. Elimination from playas by occasional flooding (Wallace and Romney 1972) would be related to root oxygen deprivation, which has been studied by Lunt et al. (1973). Hallmark and Allen (1975) studied 11 west Texas soil variables and found weak correlations of *L. tridentata* distribution with lime and gravel content. Barbour (1970) found no significant effects of pH and salinity changes across *L. tridentata* ecotone lines, although germination of *L. tridentata* was related to salinity.

Romney et al. (1973) published a volume of soil, plant, and meteorological data exhaustively describing 78 sites in the Mojave Desert and Mojave-Great Basin transition zones of the Nevada Test Site. Fifty of these sites support a *L. tridentata* population. For this study we used these data to investigate edaphological factors involved in *L. tridentata* mineral nutrition and plant size.

METHODS

Programs for multivariate statistical analyses-correlation matrices, multiple linear regression, and principal component analysis were prepared by Dixon (1971). The analyses were run for 49 of the 50 sites, because one site that lacked biomass data for *L. tridentata* was deleted.

Sum of cations and cations minus N were the sums in me/100 g of leaf K, Na, Mg, and Ca, with me N/100 g subtracted in the latter case.

"Dust" contamination of several elements was calculated using a simple linear regression line of leaf concentration of the element versus either Si or Al, whichever correlated most strongly. The residual of the equation was assumed to represent "metabolic" content (abbreviated "meta"), and the slope times the Si or Al concentration was considered contamination. (The terms *dust* and *metabolic* express one of several possible interpretations of these factors.)

Soil depth was considered either the deepest point recorded or the depth to a caliche hardpan.

RESULTS

Table 1 lists means and standard deviations of the variables on 49 *L. tridentata*-inhabited sites used in the subsequent analyses. The soils are very gravelly, high in lime, and in some cases underlain by a caliche hardpan. The pH fluctuates narrowly near 8.3. Aboveground biomass ranged from 932 to 3726 kg/ha, and *L. tridentata* biomass ranged from 9 to 1664 kg/ha. Leaf sum of cations averaged 158 me/100 g, and cations minus N averaged −10 me/100 g, indicating approx-

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TABLE 1. Averages for variables analyzed in this study. Measurements were made at 49 sites in the northern Mojave Desert.

Variable	Avg ± sd	Unit	Variable	Avg ± sd	Unit
Community parameters			*Soil variables*[a]		
Total biomass	1859 ± 770	kg/ha	Clay	4 ± 3	%
Total density	10 ± 5	thousands/ha	Silt	7 ± 4	%
Larrea biomass	714 ± 349	kg/ha	Organic C	0.3 ± 0.2	%
Larrea size	757 ± 300	g/plant	Organic	0.04 ± 0.02	%
Larrea leaf minerals			*Saturation extract*		
N	169 ± 20	me/100 g	pH A_1	8.4 ± 0.4	
P	0.21 ± 0.06	%	pH C_1	8.6 ± 0.3	
Na	0.05 ± 0.03	%	EC25	1.0 ± 0.9	mmho/cm
Si	0.3 ± 0.1	%			
K	56 ± 18	me/100 g	CEC	12 ± 4	me/100 g
Ca	80 ± 21	me/100 g	Na	3 ± 4	me/l
Mg	19 ± 6	me/100 g	K	3 ± 2	me/l
Sum of cations	158 ± 34	me/100 g	Ca	7 ± 9	me/l
Dust corrected					
sum of cations	152 ± 34	me/100 g	$SO_4^=$	1 ± 2	me/l
Cations – N	−10 ± 34	me/100	NO_3 – N	13 ± 32	ug/g
Dust Mg	4 ± 2	ug/g			
Dust Na	1.1 ±	me/100 g			
Zn	25 ± 7	ug/g	Highest Na	14 ± 20	ug/g
Cu	3.2 ± 1.9	ug/g			
Fe	384 ± 171	ug/g	Highest NO_3	67 ± 88	ug/g
Meta Fe	183 ± 125	ug/g	Highest NO_3 below A_1	50 ± 91	ug/g
Dust Fe	204 ± 98	ug/g			
Mn	40 ± 11	ug/g	*DTPA extract*		
B	79 ± 20	ug/g	Cu	0.13 ± 0.06	ug/g
Al	537 ± 261	ug/g	Fe	0.22 ± 0.17	ug/g
			$NaHCO_3$ extract		
			P	1 ± 1	ug/g

[a]All soil variables are for the C_1 horizon except pH A and those "highest" values from which the greatest value measured at the site was used.

imate equality between nitrogen and cation milliequivalents.

Variables correlating significantly (p = <0.05) with *L. tridentata* biomass and sum of cations are presented in Table 2. These independent variables "explain" generally less than 20 percent of the variability in biomass. Total leaf Fe, meta Fe, and leaf P and Zn correlated unusually strongly with the sum of cations. Of the three soil variables studied (Table 2), C_1NO_3 correlated most strongly with plant size. The C_1 refers to soil horizon.

Table 3 shows variables that correlated significantly (p = <0.05) with leaf Fe fractions. Of the soil variables, only depth and silt content correlated significantly with meta Fe, clay with dust Fe, and soil depth with overall leaf Fe. Soil Fe, as extracted by DTPA, did not correlate significantly with any leaf Fe variable.

Table 4 presents the results of multiple linear regression of independent variables versus *L. tridentata* biomass per plant and sum of cations. The analyses were run in such a way that no variable had an F-to-enter ≤ 4.0. With three variables entered, 44 percent of the plant size variability is explained, and metabolic Fe variations explained 36 percent of the sum of cations.

The first 2 of 20 principal components of

TABLE 2. Correlation coefficients (r) of selected variables correlating significantly (p = <0.05) with *L. tridentata* biomass and leaf cations.

Variables	*L. tridentata* Biomass/plant	Leaf Sum of cations
C_1pH	−0.30	0.29
C_1NO_3 μg/g	0.45	ns
Soil EC25°	0.39	ns
C_1 Ca	0.43	ns
Soil depth cm	0.39	ns
C_1 Zn	−0.36	ns
Leaf Fe	−0.36	−0.40
Meta Fe	−0.37	−0.56
Leaf P	ns	0.47
Leaf Zn	ns	0.50

TABLE 3. Correlation coefficients of variables significantly ($p = < 0.05$) correlated with leaf Fe fractions and DTPA extractable soil Fe.

	Leaf Fe	Dust Fe	Meta Fe	Soil Fe
		r		
Sum of leaf cations	–0.40	ns	–0.56	ns
Leaf Na	0.39	0.54	ns	ns
Leaf K	–0.50	ns	–0.56	ns
Leaf Ca	–0.31	ns	–0.47	ns
Leaf Si	0.70	0.87	ns	ns
Leaf Al	0.70	1.00	ns	ns
Leaf Mn	0.48	0.59	ns	ns
Leaf P	ns	ns	–0.43	ns
Leaf Zn	ns	ns	–0.46	ns
Dust Fe	0.70	1.00	ns	ns
Meta Fe	0.82	ns	1.00	ns
Larrea-Biomass/plant	–0.36	ns	–0.37	ns
Overall Biomass/ha	–0.30	ns	–0.32	ns
Depth	–0.32	ns	–0.35	ns
C_1 Clay	ns	0.31	ns	0.40
C_1 Silt	ns	ns	0.30	0.47
Organic C	ns	ns	ns	0.55
Organic N	ns	ns	ns	0.53
Water holding capacity	0.29	ns	ns	0.47

L. tridentata leaf mineral composition accounted for 46 percent of the total variance. Variables scoring highest on the first component were leaf Fe and sum of cations. Those scoring highest on the second component were cations minus N and leaf Al. Analyses of community and soil variables showed a diffuse distribution of variance among the factors studied.

Soil pH correlated significantly with percent clay ($r = +0.30$) and saturation extract Mg ($r = -0.40$), besides the correlations with *L. tridentata* size and sum of cations (Table 2). Both saturation extract and paste pH were measured. Paste pH did not correlate significantly with sum of cations and was not considered for the bulk of this study.

DISCUSSION

There are a multitude of variables affecting size of *L. tridentata* plants in the field. Several important factors not considered here include rainfall, plant age, incidence of grazing, and competition with neighboring shrubs. Because these data are from the field, no variable was controlled. We thus feel justified in imputing significance to variables that can explain just 10 to 20 percent of the variability in plant size.

Of the three factors correlating strongest with plant size, only the first, C_1NO_3 concentration, is easily explained. The correlation implies that NO_3 levels, measured at single points, limit plant growth, and that they are

TABLE 4. Multiple linear regressions of independent variables affecting *Larrea tridentata* biomass* per plant and leaf sum of cations.**

Step	Variable added	Coefficient	Multiple r^2	Constant
A. Biomass per plant (g) = 3.47 (C_1NO_3) – 1.13 (Meta Fe) – 376.8 (pH) ÷ 4139				
1.	C_1NO_3	3.47	0.20	688
2.	Meta Fe	–1.13	0.33	865
3.	C_1pH	–376.8	0.44	4139
B. Sum of leaf cations, me/100 g = 181.5 – 0.16 (Meta Fe)				
1.	Meta Fe	–0.16	0.36	181.5

No other independent variables had significant F value to enter.

Larrea tridentata biomass per hectare was deleted.
**Deleted variables were cation-N, leaf K, leaf Ca, and leaf Mg.

representative of those over the whole 100 m^2 transect used to determine plant size. The data are also consistent with the distribution of shrub roots that are primarily in the Band C horizons.

It is somewhat surprising that the small variations in pH should correlate with *L. tridentata* size. The hydrogen ion concentration ranges from 10^{-8} to 10^{-9} *M*, though other cations are present at 10^{-3} *M* (Table 1). Because the correlation was negative, it is possible the higher soil pH values tend to inhibit *L. tridentata* growth.

No attempt was made to measure rhizosphere pH, though data of Turner (1972) suggest that in desert soils rhizosphere pH is reduced even in these heavily calcareous soils. Smiley (1974) found that lime buffered soil against pH changes caused by nitrogen uptake, but Stark (1973) and Hanawalt and Whittaker (1977) found that an acid soil extract represented plant-available nutrients better than neutral extracts.

Van Egmond and Aktas (1977) reported that Fe-efficient soybeans excrete more H^+ into the medium than do Fe-inefficient varieties. However, we found no correlation between soil pH and leaf Fe variables.

Larrea tridentata should certainly be considered an Fe-efficient species. The negative correlation between leaf Fe and plant size may be explained in several ways, but it is not consistent with suggestions of Fe deficiency affecting size. Indeed, the correlation reflected a cause-effect relationship, and Fe toxicity would be indicated.

Iron uptake, translocation, and physiology have been extensively studied, but may still be characterized as poorly understood (Thorne and Wallace 1944, Brown 1956, Khadr and Wallace 1964, Brown and Ambler 1974, Jones 1976). A frequent observation has been an association of Fe with K uptake (Thorne and Wallace 1944, Brown 1956, Hernando and Sanfuentes 1976). In this study we found correlation of leaf Fe variables with both leaf K and *L. tridentata* biomass, but not between biomass and leaf K. The strong negative association of meta Fe with both leaf K and sum of cations are consistent with the hypothesis that lime-induced chlorosis is related to cation-anion balance and internal leaf pH (Wallace et al. 1976). The positive correlation of leaf Zn with sum of cations (r = +0.50), and the negative correlation of meta Fe (r = –0.56) suggest an Fe-Zn interaction.

One implication of these findings is that the Fe nutrition of *L. tridentata* growing on calcareous soils is similar to, but different in degree from, that of species exhibiting lime-induced chlorosis.

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